Die another day; Growth model reveals high natural survival rates in loggerhead sea turtles

A THESIS
SUBMITTED TO THE FACULTY OF
UNIVERSITY OF MINNESOTA
BY

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTERS OF SCIENCE

Advised by Paul A. Venturelli

July 2017

Acknowledgements

First and foremost, thank my committee; Paul Venturelli, Seth Stapleton, and Todd Arnold. Paul, I cannot thank you enough for responding to an email regarding sea turtle research and for reaching out to me again after attempts to find funding failed and I decided to take a year off of school. You gave me the opportunity to study a marine organism while staying close to the people who mean the most to me. With limited statistics and no coding background, this project challenged me every step of the way. Your patience and guidance were invaluable over the past 2 years. I now have a skillset that allows me to continue sea turtle research from the Midwest. You also kept your end of the bargain and allowed me to travel for a month of field work which resulted in one of the best experiences thus far in my career. Seth, I cannot thank you enough for being a sea turtle expert who also decided to live in Minnesota. Your turtle expertise has been so valuable over the past 2 years. I would also like to thank you for letting me join the Jumby Bay field team for part of the 2016 season. I am so grateful for the time I was able to spend in Antigua. It is an incredible project and I feel so fortunate to have the opportunity to work with such a fantastic dataset. Todd, thank you for providing a fresh prospective on this project. Your questions regarding the model coding challenged me to think critically and enhanced my knowledge of how this model functions.

This project would not have been possible without funding support from the University of Minnesota and those willing to share their data and expertise. I would like to extend a thank you to Larisa Avens and Melissa Snover at NOAA for their collection of the Northwest Loggerhead data and their willingness to share it with me for this new

analysis. Karen Bjorndal and Alan Bolten at the University of Florida- Gainesville also provided invaluable knowledge and guidance through this project.

I would also like to thank my family. Mom and Dad, your endless support through my field work travels and pursuit of this degree has been incredible. You have always encouraged me to chase my dream, no matter how far away it may take me. You undoubtedly would have been supportive of my graduate school ambitions no matter where I chose to attend, but I am so thankful that I was able to stay so close to home. I can't thank you enough for all that you have done for me. To my amazing fiancé, your support over the past 4 years has me at a loss for words. Regardless of our conflicting, busy schedules, you have always been there for me. You have been supportive of my decision to go back to school, my month-long field work excursions to foreign countries, and sacrificed sleep to help take care of the puppy while I need to be working. You have worked so hard to provide for us so that I could focus on my classes and thesis work. I can't tell you how much that means to me. You have had a larger role in the success of this project than you realize.

Abstract

Accurate survival estimates are essential to sea turtle conservation but difficult to estimate due to anthropogenic mortality and confounding factors such as tag loss and emigration. The Lester Growth Model allows for the estimation of sex-specific adult natural survival rates (the rate that a population would experience independent of human influence) from length-at-age and maturity data. I applied this model to individual loggerheads of the Northwest Atlantic subpopulation. Both male and female annual natural survival rates were estimated to be 96-97%; ~0.14 higher than published total survival values. This result was corroborated by a population model designed to estimate a range of possible adult survival rates. These natural survival rates, in conjunction with published rates, allow for the estimation of anthropogenic mortality and assessment of the impact of confounding factors on mark-recapture studies. It is likely that this technique can be leveraged for other loggerhead populations and sea turtle species.

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Introduction

Effective sea turtle conservation requires accurate estimates of mortality. Total mortality is a combination of natural mortality, the rate that a population experiences independent of human influence, and anthropogenic mortality (e.g., bycatch and illegal harvest). Mortality can be difficult to estimate because sea turtles are long-lived, late-maturing, and highly migratory. Mortality is typically estimated as finite survival via mark-recapture (Frazer 1983, Crouse et al. 1987, Hedges 2007, Monk et al 2011, Phillips 2014, Penaloza et al 2014); however, natural and anthropogenic sources of mortality can be difficult to disentangle and may be confounded by tag loss or emigration (Arnason & Mills 1981, Seber 1982, Monk et al. 2011, Phillips 2014).

The Lester growth model (LGM) estimates the natural mortality rate of adults from the change in growth rate that occurs with maturity (Lester et al. 2004). This model is based on the theory that investment in reproduction is an evolved trait that trades off with natural mortality. In general, adults invest in reproduction at the expense of growth and survival (Stearns 1989, Stearns 1992). This trade-off with growth has been identified in turtles (Congdon and Gibbons 1990, Congdon et al. 1993) and other reptiles (e.g., 88 species of lizards; Tinkle 1970). The degree to which adult growth slows relative to immature growth in the LGM is indicative of investment in reproduction and therefore natural mortality rate (Lester et al. 2004). The LGM has been used to estimate the natural mortality rate of boney fishes and sharks (e.g., Clark and Hare 2006, Lester et al. 2014, Moe 2015, Uusi-Heikkilä et al. 2015, Chavarie et al. 2016, Matthias et al. 2016) but has yet to be applied to sea turtles.

Sea turtles meet the key assumptions of the LGM. They mature late and have long reproductive life spans (Hays & Speakman 1991, Congdon et al. 1993, Scott et al. 2012). Growth is indeterminate (Parham and Zug 1997, Bjorndal et al. 2013), and body mass tends to increase with the cube of body length (Hitchins et al. 2004, Meylan et al. 2011). Clutch size also increases with body size (Hays and Speakman 1991, van Buskirk and Crowder 1994), and the exponent of the metabolism-mass relationship is 0.70±0.10 (n = 49) and 0.78±0.09 (n = 32) for active and resting sea turtles, respectively (my reanalysis of Table 2 in Wallace & Jones 2008). Therefore, the LGM may be an effective means of using length-at-age and maturity data to estimate sea turtle natural mortality rates.

I used the LGM to estimate the natural mortality rate of loggerhead sea turtles (*Caretta caretta*) in the Northwest Atlantic, and then compared this estimate to mortality estimates derived from a population model and the literature. Globally, loggerhead sea turtles are listed as vulnerable (Casale et al. 2015, Ceriani et al. 2015). Loggerheads in this dataset were from the Northwest Atlantic sub-population, which includes nesting populations from Florida north to the New England region of the United States, and are listed under “Least concern” by the IUCN. This sub-population is well-studied, including a dataset of length-at-age and age-at-maturity (described in Avens et al. 2015), and estimates of key life history traits (e.g., survival, fecundity, remigration). Mark-recapture based estimates of annual adult survival rates in this sub-population range from 73-85% (SEFSC 2009), but may be confounded by tag loss and emigration (Monk et al. 2011, Phillips 2014). Mark-recapture for turtles does not estimate natural survival, and I am unaware of uncofounded estimates of total survival.

Methods

Sea turtle data

I obtained loggerhead sea turtle length-at-age, sex, and maturity data from a large dataset that is maintained by the National Oceanic and Atmospheric Administration and populated with assistance from the National Sea Turtle Stranding and Salvage Network. Dead or euthanized turtles in this dataset were necropsied for sex determination (when possible), and to collect humeri cross sections for skeletochronological age analysis and length back-calculation (see Avens et al. 2015 for details). When possible, age at maturity was also determined by rapprochement (decrease in spacing) of lines of arrested growth. The dataset contained growth data from 299 individuals from Massachusetts at the northern end of the range to Florida in the south, as well as the Azores. Age at maturity (T) was estimated for 47 of these individuals (24 males and 23 females).

I applied the LGM to loggerheads for which there were estimates of T, and three or more length-at-age estimates on either side of T. Although ontogenetic shifts in diet and habitat can lead to polyphasic growth in juvenile loggerheads (Chaloupka 1998), LGM fits should be limited to the final immature phase (Lester et al. 2004) (Figure 1 Panels a & b). To meet this criterion objectively, I fit a linear model to length data from the three oldest immature ages, and then added data from younger ages in sequence until either all immature ages were included, or the next immature age was an influential outlier according to a combination of high leverage and Cook's distance > 0.5 (Figure 1b).

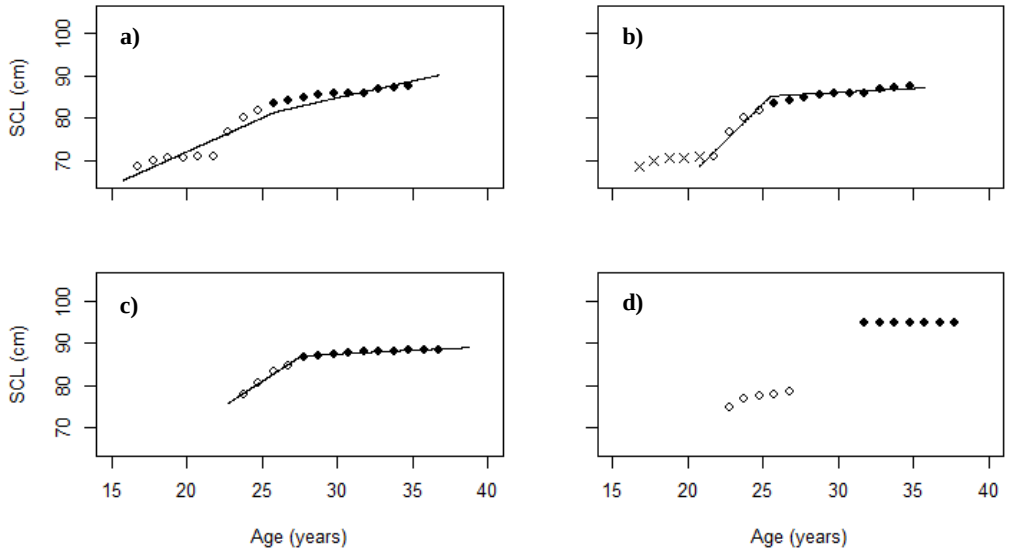

Figure 1. Examples of fits produced by the Lester growth model showing a) a fit that ignored variable growth rates in the juvenile phase (loggerhead 34), and b) the fit to data from loggerhead 34 after juvenile age truncation, c) a typical fit (loggerhead 50), and d) data for which the model did not converge (loggerhead 249). Open and closed circles are immature and mature data points, respectively, and x's are immature data points that were excluded from the analysis via age truncation.

Natural Mortality and Survival Estimates

I estimated natural mortality and survival from parameters of the LGM via a mixed model that fit the LGM to back-calculated length-at-age data (Vigliola & Meekan 2009). I included slope and intercept as both fixed and random effects, which allowed me to extract both population- and individual-level parameter estimates. Consistent with the LGM, I fit different growth functions for the juvenile and adult phases. I fit a line to immature length-age data to generate individual estimates of *h* (slope, growth in cm/year) and the y-intercept (the hypothetical length in cm at 0 years of age). I used these parameters to calculate t_1 (x-intercept = -(y-intercept/h), the hypothetical age in years at 0 cm length).

I then fit the LGM form of the von Bertalanffy curve to mature length-at-age data using the individual t_1 and h estimates from the immature (linear) fit. This curve is given by

(1) $L_t = (h/(exp(K)-1)) * (1 - exp(K * ((T + log(1 - (exp(K)-1) * (T - t1))/K) - t)))$,

where t is age in years and K is the von Bertalanffy growth coefficient that describes the annual rate of deceleration of growth (/year).

I used two methods to estimate the instantaneous mortality rate of adult loggerheads from LGM parameters:

(2.1) $$M_1 = -\ln\left(1 - \frac{3(e^K)-1}{1.18}\right),$$

which combined equations 3.3 and 4.6 in Lester et al. (2004), and

(2.2) $$M_2 = \frac{2}{(T - t_1 + 1)}$$

(Appendix A in Lester et al. (2014)). I calculated M_1 and M_2 for males and females separately by extracting individual K and t_1. To facilitate comparisons with the loggerhead literature, which reports finite annual survival rates (S), I then converted M_1 and M_2 to finite annual survival rates via e^{-M}, where M is either M_1 or M_2.

Matrix population estimate

Because the natural mortality or survival rate of adult loggerheads is unknown, I used a stochastic, stage-based projection matrix to generate a second, independent estimate of likely values. This matrix follows a female-only, Lefkovitch design (Crouse et al. 1987) comprising four life stages (Oceanic juvenile, small benthic juvenile, large benthic juvenile, and adult), and a fecundity parameter that is defined as:

(3.1) $$\frac{(NF\ x\ EN\ x\ ES\ x\ PF)}{RI},$$

where NF is the number of nests per female, EN is the number of eggs per nest, ES is egg survival, PF is the proportion of female offspring (sex ratio) and RI is the remigration interval. The matrix model took the form

$$\begin{bmatrix} P_{OJ} & 0 & 0 & F \\ G_{OJ} & P_{SB} & 0 & 0 \\ 0 & G_{SB} & P_{LB} & 0 \\ 0 & 0 & G_{LB} & s_A \end{bmatrix},$$

where OJ = oceanic juvenile, SB = small benthic juvenile, LB =large benthic juvenile, A =adult , and F is fecundity. P is the probability of surviving and remaining in the same life stage as determined by

(3.2) $$P_i = \left(\frac{1-s_i^{d_i-1}}{1-s_i^{d_i}}\right) s_i \ ,$$

G is the probability of surviving and moving to the next life stage as determined by

(3.3) $$G_i = \frac{s_i^{d_i}\left(1-s_i^{d_i}\right)}{1-s_i^{d_i}} \ .$$

In both of these equations, d = stage duration, s = annual survival probability (also used in the adult stage of the matrix) and i = life stage. Model structure and parameter values (Appendix A) were taken from a National Oceanic and Atmospheric Administration report on nesting populations of Atlantic loggerheads (SEFSC 2009). I assumed that finite annual adult survival was unknown. I incorporated stochasticity into the projection matrix by randomly drawing values for all parameters except adult survival from either a truncated normal or uniform distribution (Table 1). I used relatively narrow normal distributions (shape parameter = 8; SERSC 2009) to avoid unrealistic parameter (i.e., life

history) combinations and over-dispersed adult survival estimates. I estimated adult survival iteratively to generate 10,000 estimates of adult survival by analyzing the projection matrix (Stubben and Milligan 2007) until the finite rate of population increase (λ) was equal to 1 (i.e., zero population growth). Assuming $\lambda=1$ resulted in conservative survival estimates given that the Northwest Atlantic sub-population estimates have been increasing in recent years. In the event that anthropogenic mortality biased juvenile survival rates low (and therefore biased adult survival estimates high), I estimated a second set of adult survival rates by only considering survival rates from the upper half of the normal distributions of oceanic, small benthic, and large benthic juveniles.

Results

The LGM produced estimates of adult *M* for 16 (seven male, nine female) loggerhead sea turtles in the NOAA dataset. Another three turtles met my data requirements, but I was unable to estimate *M* due to atypical growth patterns that generated errors during the fitting procedure (e.g., Figure 1d). For individuals with successful fits, the mean *T* values were 36.04±7.39 years for males and 33.42±9.39 years for females. For males, t_1 and *K* were estimated at -37.46±32.23 years and .02±.004, respectively. For females, these estimates were -52.13±40.09 years and .02±.008, respectively. According to Lester's first method, finite adult natural mortality of males and females was 4.15±1.03 and 3.99±2.17%, respectively. These corresponded to finite annual natural survival rates of 95.85±1.03 and 96.01±2.17%. Lester's second method generated similar estimates: 3.13±1.37% (96.87±1.37%) and 2.96±1.89% (97.04±1.89%).

These survival rates produce an overall natural survival mean and standard deviation of 96.44±1.67%.

My matrix population model predicted a left-skewed distribution of adult survival rates with a median of 96.77% (Figure 2a). This distribution shifted to lower values of adult survival (median =92.67%) when I excluded the lower 50% of oceanic juvenile, small benthic juvenile, and large benthic juvenile survivals under the assumption that they were biased low due to emigration, tag loss, and anthropogenic mortality (Figure 2b).

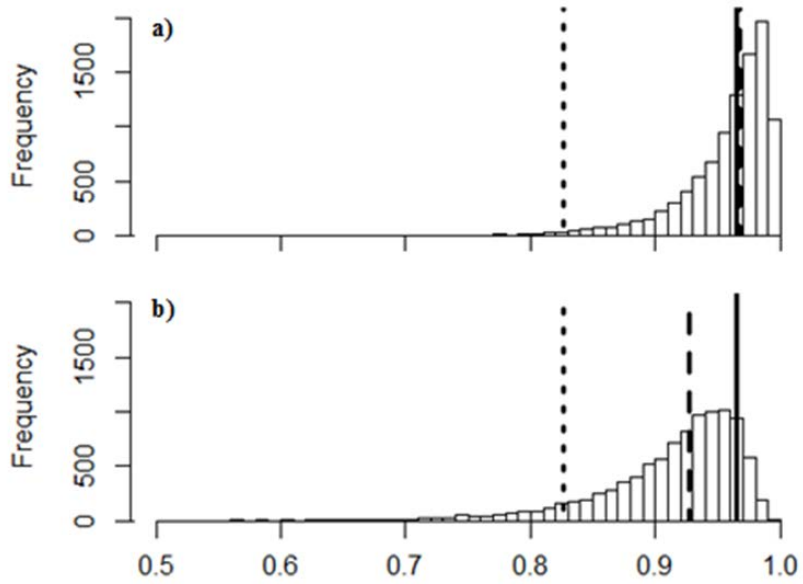

Figure 2. Adult loggerhead survival distributions produced by the matrix model given a) upper half distributions of all juvenile survival rates, and b) full juvenile survival distributions. Dotted line indicates the average survival reported in the literature, solid line indicates the average natural survival produced by the LGM, and the dashed line indicated the median survival produced by the matrix model.

The LGM life history-based estimates of annual adult survival were only 0-0.04 higher than the median values produced by the matrix population model. Field-based survival estimates from the literature were 0.138 lower than life history-based estimates

of natural survival, and less than model-based predictions in 90.53-97.81% of simulations.

Discussion

The LGM predicted finite annual natural mortality rates of 3-4% for the Northern West Atlantic sub-population of loggerheads, which correspond to annual natural survival rates of 96-97%, for both sexes. This is the first published estimate of male-only survival rate for this sub-population. Estimation of survival via mark-recapture is difficult because male sea turtles do not come ashore to nest. However, survival rates tend to be similar when reported for both males and females. For example, both male and female survival were 87.5% for a population of loggerheads on the Great Barrier Reef (Chaloupka and Limpus 2002). Although the production of similar survival rates for males and females by this model implies similar investment in reproduction, it is difficult to reconcile this conclusion with sea turtle biology. Whereas female investment in reproduction includes gonadal development and continues with egg production and the costs associated with laying eggs throughout life, the majority of male investment is limited to morphological changes that occur at maturity (e.g. Spotila 2004). If female turtles invest more in reproduction, then similar estimates of investment in reproduction could be due to more frequent reproduction and higher energy expenditure during mating by males than females. An alternative hypothesis is that the change in adult male growth rate was due, not only to investment in reproduction, but also lower growth efficacy and a higher metabolic rate (Rennie et al. 2008, Rennie & Venturelli, 2015). Differing growth

efficacy and metabolism between males and females has been observed in fish, but has not been evaluated in sea turtles.

My results also suggest that the natural survival of female loggerheads is nearly 0.14 higher than published total survival rates (Figure 3). Given that these published rates are rarely sufficient to sustain Northwest Atlantic loggerheads (Figure 2), I attribute the difference between life history- and field-based estimates to, not only anthropogenic mortality, but also tag loss and emigration. This hypothesis is supported by the fact that published survival rates for this population do not support observed adult longevity. For example, following Lawless (1982), the 0.81% annual survival probability published by Frazer (1983) implies an average adult lifespan of less than 5 years (Chaloupka and Limpus 2002). Conversely, our mean natural survival estimate of .9644 predicts an average adult life span of 27.6 years (range 23.6-33.3 years). This life history-based estimate is more in line with the observed range of adult life spans within the loggerhead data set (4-46 years) (Avens et al. 2015). Lifespans on the lower end of this range likely reflect the fact that many loggerheads enter the data set via anthropogenic (i.e., “early”) sources of mortality.

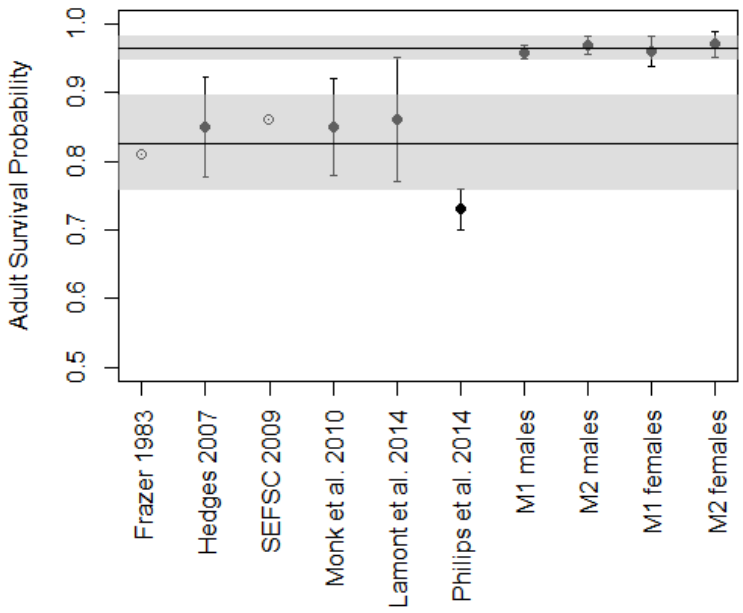

Figure 3. Comparison of published survival rates and natural survival rates estimated via the LGM model. Mean survival rate from published literature and LGM results shown as horizontal lines. Associated pooled standard deviations (gray regions) were calculated from available standard deviations. Studies without reported standard deviations are identified by hollow points.

The prospect of predicting natural survival from length-at-age and maturity data is encouraging, but I note three caveats. First, although the LGM and population model generated similar natural survival estimates, the "true" natural survival rate of Northwest Atlantic loggerheads is unknown. Validating these estimates requires unbiased field data, efforts to correct for biases (e.g. multiple tags, drill patterns in shell), or alternative estimation techniques. Second, the matrix model that I used to independently estimate adult survival assumed that all other parameter estimates were accurate. This may not be the case for early-stage survival rates, which are even more challenging to estimate than adult survival rates. However, model results were robust when juvenile survival rates were constrained to large values (Figure 3b), and a *post-hoc* elasticity analysis suggests that population growth rate is relatively insensitive to juvenile survival rates (Figure 4).

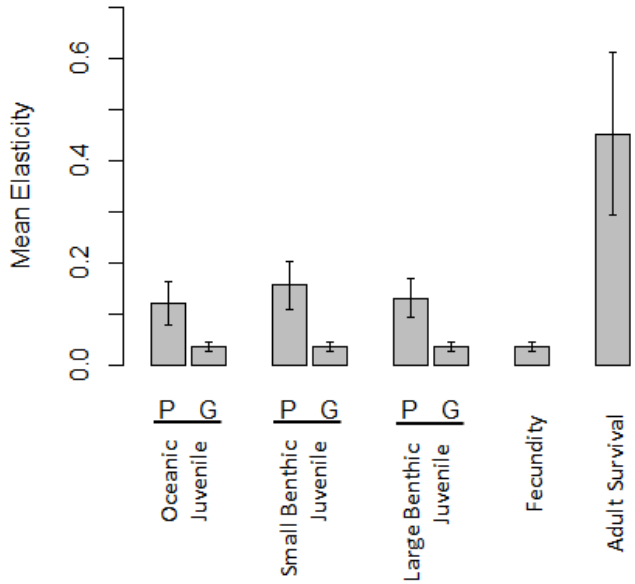

Figure 4. Mean elasticity of survival and fecundity parameters from the full juvenile distribution matrix model and associated standard deviations where P is probability of surviving and staying within the same life stage, and G is the probability of surviving and moving to the next life stage.

The final caveat is that I used the LGM to estimate adult survival from life history traits that may or may not be density-dependent. Density-dependent growth typically occurs as a result of changes in per-capita food availability, and would affect K in equation 2.1 and t_1 in equation 2.2. Density-dependent growth has been observed in a population of green turtles (*Chelonia Mydas*) that experienced large changes in abundance over an 18-year period (Bjorndal et al. 2000). To our knowledge, density dependent growth in loggerheads has not been evaluated. If individuals of this population are experiencing density dependent growth, the natural survival estimates produced by the LGM may not be impacted. Lester et al. (2014) showed analytically that investment in reproduction (which is proportional to K) may be only weakly density-dependent. However, their solution assumed a relatively fixed size-at-maturity. In a population of

captive sea turtles, size-at-maturity was variable as a result of variable age-at-maturity and pre-maturity growth rate (Bjorndal et al. 2012). The parameter T, then, in equation 2.2, may also be influenced by density-dependent factors. While density-dependence may influence the range of these parameter estimates, the LGM still produced high natural survival rates across all values.

Having estimates of both natural survival and total survival allows us to estimate the impact that confounding factors have on estimation via mark-recapture. Many mark-recapture studies attempt to account for tag loss and emigration, but they are often assumed negligible because of the difficulty associated with measuring these rates (Monk et al. 2011, Philips et al. 2014, Hedges et al. 2007). Applying this assumption to our data puts anthropogenic mortality for this population at nearly 14%. This scenario is unlikely for a sub-population that has exhibited an increase in the number of nesting female in recent years, and is classified as "least concern" (Ceriani & Meylan 2015). This matrix model also suggests that such a scenario is likely to result in population declines. Anthropogenic mortality rates in fisheries are considered sustainable when they are equal to or less than M (Alverson & Pereyra 1969, Gulland 1970, Gulland 1971, Lester et al. 2014). This has not been established for sea turtles; but if they also follow this rule of thumb, a more likely scenario for this sub-population is that anthropogenic mortality is equal to or less than the estimated 3-4% annual natural mortality rate. If so, then I hypothesize that the remaining 10-11% discrepancy between life history- and field-based survival estimates is due to tag loss and emigration. This hypothesis is supported by the general relationship between survival and maturity among reptiles (Shine and Iverson

1995). Frazer's estimate of 81% adult survival is an outlier to this trend; freshwater turtles of a comparable age-at-maturity have been found to experience adult survival of 97% (Shine and Iverson 1995).

My results suggest that the LGM can be applied to length-at-age and maturity data to estimate the natural mortality rate of a loggerhead population. This rate had not yet been estimated for a population of sea turtles and can be used in conjunction with mark-recapture studies to assess anthropogenic mortality and the influence of confounding factors. The LGM has the potential for further application to other species and populations of sea turtles, and perhaps a broader range of reptiles and amphibians. Collecting data to assess life history characteristics on long-lived, migratory species such as sea turtles is time-consuming and labor-intensive. Therefore, it is in our best interest to leverage existing data in new ways. The LGM is one such technique that can easily be expanded to other population and species for which longitudinal growth data are available. The LGM can also be used to estimate age at sexual maturity (Honsey et al. 2017), and could be as validation for current maturity estimates and techniques.

References

Alverson, D. L., and W. T. Pereyra. 1969. Demersal fish explorations in the Northeastern Pacific Ocean: an evaluation of exploratory fishing methods and analytical approaches to stock size and yield forecasts. Journal of the Fisheries Research Board of Canada 26:1985–2001.

Arnason, A.N. and Mills, K.H., 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. Canadian Journal of Fisheries and Aquatic Sciences, 38(9), pp.1077-1095.

Avens, L., Goshe, L.R., Coggins L. Snover, M.L., Pujuelo, M., Bjorndal, K.A., Bolten, A.B, 2015. Marine Biology 162: 1749

Berry, J., & Shine, R. 1980. Sexual Size Dimorphism and Sexual Selection in Turtles (Order Testudines). *Oecologia*, *44*(2), 185-191.

Bjorndal, K.A., Schroeder, B.A., Foley, A.M., Witherington, B.E., Bresette, M., Clark, D., Herren, R.M., Arendt, M.D., Schmid, J.R., Meylan, A.B. and Meylan, P.A., 2013. Temporal, spatial, and body size effects on growth rates of loggerhead sea turtles (Caretta caretta) in the Northwest Atlantic. Marine biology, 160(10), pp.2711-2721.

Bjorndal, K.A., Bolten, A.B. and Chaloupka, M.Y., 2000. Green turtle somatic growth model: evidence for density dependence. Ecological Applications, 10(1), pp.269-282.

Casale, P. & Tucker, A.D., 2015. Caretta caretta. The IUCN Red List of Threatened Species

Ceriani, S.A. & Meylan, A.B., 2015. *Caretta caretta* (North West Atlantic subpopulation). The IUCN Red List of Threatened Species

Chaloupka, M., 1998. Polyphasic growth in pelagic loggerhead sea turtles. Copeia, 1998(2), pp.516-518.

Chaloupka, M., & Limpus, C. (2002). Survival probability estimates for the endangered loggerhead sea turtle resident in southern Great Barrier Reef waters. Marine Biology, 140(2), 267-277.

Chavarie, L., Howland, K., Venturelli, P., Kissinger, B.C., Tallman, R. and Tonn, W., 2015. Life-history variation among four shallow-water morphotypes of lake trout from Great Bear Lake, Canada. Journal of Great Lakes Research.

Clark, W. G., and S. R. Hare., 2006. Assessment and management of Pacific Halibut: data, methods, and policy. International Pacific Halibut Commission Scientific Report 83.

Congdon, J.D., Dunham, A.E. and van Loben Sels, R.C., 1993. Delayed sexual maturity and demographics of Blanding's Turtles (*Emydoidea blandingii*): Implications for conservation and management of long-lived organisms. Conservation Biology, 7(4), pp.826-833.

Congdon, J., Gibbons, J.W., 1990. The evolution of turtle life histories, p. 45-54. In: Life history and
ecology of the slider turtle. J. W. Gibbons (ed.).Smithsonian Institution Press, Washington, DC.

Crouse, D.T., Crowder, L.B. and Caswell, H., 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology, 68(5), pp.1412-1423.

Frazer, N.B., 1996. Demography and life history evolution of the Atlantic loggerhead sea turtle, *Caretta caretta*. UMI Dissertation Services.

Godley, B. J., Broderick, A. C., Frauenstein, R., Glen, F., & Hays, G. C. 2002. Reproductive seasonality and sexual dimorphism in green turtles. *Marine Ecology Progress Series*, *226*, 125-133.

Gulland, J. A. 1970. The fish resources of the ocean. Fisheries Technical Paper Number 97. Food and Agricultural Organization, Rome, Italy.

Gulland, J. A. 1971. The fish resources of the ocean. Fishing News Books, West Byfleet, UK.

Hays, G.C. and Speakman, J.R., 1991. Reproductive investment and optimum clutch size of loggerhead sea turtles (*Caretta caretta*). The Journal of Animal Ecology, pp.455-462.

Hedges, M.E., 2007. Development and application of a multistate model to the northern subpopulation of loggerhead sea turtles (*Caretta caretta*) (Doctoral dissertation, Virginia Polytechnic Institute and State University).

Hitchins, P.M., Bourquin, O., Hitchins, S. and Piper, S.E., 2004. Biometric data on hawksbill turtles (*Eretmochelys imbricata*) nesting at Cousine Island, Seychelles. Journal of Zoology, 264(04), pp.371-381.

Honsey, A. E., Staples, D. F., & Venturelli, P. A. 2017. Accurate estimates of age at maturity from the growth trajectories of fishes and other ectotherms. *Ecological Applications*, *27*(1), 182-192.

Koch, V., Nichols, W.J., Peckham, H. and de la Toba, V., 2006. Estimates of sea turtle mortality from poaching and bycatch in Bahia Magdalena, Baja California Sur, Mexico. Biological Conservation, 128(3), pp.327-334.

Lamont, M.M., Fujisaki, I. and Carthy, R.R., 2014. Estimates of vital rates for a declining loggerhead turtle (*Caretta caretta*) subpopulation: implications for management. Marine biology, 161(11), pp.2659-2668.

Lawless, J.F., 1982. Statistical models and methods for lifetime data. Wiley, New York.

Lester, N.P., Shuter, B.J. and Abrams, P.A., 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. Proceedings of the Royal Society of London B: Biological Sciences, 271(1548), pp.1625-1631.

Lester, N.P., Shuter, B.J., Venturelli, P. and Nadeau, D., 2014. Life-history plasticity and sustainable exploitation: a theory of growth compensation applied to walleye management. Ecological Applications, 24(1), pp.38-54.

Matthias, B.G., Ahrens, R.N.M., Allen, M.S., Lombardi-Carlson, L.A. and Fitzhugh, G.R., 2016. Comparison of growth models for sequential hermaphrodites by considering multi-phasic growth. Fisheries Research, 179, pp.67-75.

Meylan, P.A., Meylan, A.B. and Gray, J.A., 2011. The ecology and migrations of sea turtles 8. Tests of the developmental habitat hypothesis.

Moe, B., 2015. Estimating Growth and Mortality in Elasmobranchs: Are we doing it correctly?

Monk, M.H., Berkson, J. and Rivalan, P., 2011. Estimating demographic parameters for loggerhead sea turtles using mark–recapture data and a multistate model. Population ecology, 53(1), pp.165-174.

Parham, J.F. and Zug, G.R., 1997. Age and growth of loggerhead sea turtles (*Caretta caretta*) of coastal Georgia: an assessment of skeletochronological age-estimates. Bulletin of Marine Science, 61(2), pp.287-304.

Parker, G.A. 1992. The evolution of sexual size dimorphism in fish. J Fish Biol 41:1–20.

Peñaloza, C.L., Kendall, W.L. and Langtimm, C.A., 2014. Reducing bias in survival under nonrandom temporary emigration. Ecological Applications, 24(5), pp.1155-1166.

Phillips, K.F., Mansfield, K.L., Die, D.J. and Addison, D.S., 2014. Survival and remigration probabilities for loggerhead turtles (*Caretta caretta*) nesting in the eastern Gulf of Mexico. Marine biology, 161(4), pp.863-870.

Rennie, M. D., Purchase, C. F., Lester, N., Collins, N. C., Shuter, B. J. and Abrams, P. A. 2008. Lazy males? Bioenergetic differences in energy acquisition and metabolism help to explain sexual size dimorphism in percids. Journal of Animal Ecology, 77: 916–926.

Rennie, M. D., & Venturelli, P. A. 2015. The Ecology of Lifetime Growth in Percid Fishes. In *Biology and Culture of Percid Fishes* (pp. 499-536). Springer Netherlands.

Scott, R., Marsh, R. and Hays, G.C., 2012. Life in the really slow lane: loggerhead sea turtles mature late relative to other reptiles. Functional Ecology, 26(1), pp.227-235.

Seber, G.A.F., 1982. The estimation of animal abundance.

SEFSC, 2009. An Assessment of Loggerhead Sea Turtles to Estimate Impacts of Mortality Reductions on Population Dynamics. NMFS Southeast Fisheries Science Center Contribution PRD-08/09-14.

Shine, R. and Iverson, J.B., 1995. Patterns of survival, growth and maturation in turtles. Oikos, pp.343-348.

Spotila, J.R., 2004. *Sea turtles: A complete guide to their biology, behavior, and conservation*. JHU Press.

Stearns, S.C., 1989. Trade-offs in life-history evolution. Functional ecology, 3(3), pp.259-268.

Stearns, S.C., 1992. The evolution of life histories (Vol. 249). Oxford: Oxford University Press.

Stubben, C.J. and Milligan, B.G., 2007. Estimating and Analyzing Demographic Models Using the popbio Package in R. Journal of Statistical Software 22:11

Tinkle, D.W., Wilbur, H.M., Tilley, S.G., 1970. Evolutionary Strategies in Lizard Reproduction: Evolution, Vol. 24, No. 1

Uusi-Heikkilä, S., Whiteley, A. R., Kuparinen, A., Matsumura, S., Venturelli, P. A., Wolter, C., Slate, J., Primmer, C. R., Meinelt, T., Killen, S. S., Bierbach, D., Polverino, G., Ludwig, A. and Arlinghaus, R. 2015. The evolutionary legacy of size-selective harvesting extends from genes to populations. Evolutionary Applications, 8: 597–620

van Buskirk J., Crowder L.B., 1994. Life-history variation in marine turtles. Copeia 1994:66–81

Vigliola, L. and Meekan, M.G., 2009. The back-calculation of fish growth from otoliths. In Tropical fish otoliths: information for assessment, management and ecology (pp. 174-211). Springer Netherlands.

Wallace, B.P. and Jones, T.T., 2008. What makes marine turtles go: a review of metabolic rates and their consequences. Journal of Experimental Marine Biology and Ecology, 356(1), pp.8-24.

Appendix A.

Table A1. Range of values for each parameter used to incorporate stochasticity in the survival matrix model. All parameters required normal distributions with the exception of R, which required a uniform distribution. These distributions, as well as published studies used to determine values, were taken from pages 4-12 of the 2009 NOAA Report (SEFSC 2009).

Parameter	Minimum	Nominal	Maximum
Eggs per nest (EN)	89	109	125
Nests per female (NF)	2	5	8
Egg survival (E)	.11	.53	.8
Proportion of female offspring (PF)	.35	.5	.8
Remigration interval (years) (R)	2.75	3.185	3.62
Oceanic juvenile stage duration (years)	10	13	18
Oceanic juvenile survival (PJ)	.588	.744	.878
Small benthic juvenile stage duration (years)	9	10	12
Small benthic juvenile survival (SB)	.74	.83	.89
Large benthic juvenile stage duration (years)	4	7	12
Large benthic juvenile survival (LB)	.74	.835	.925